Table 3

Summary of species and number of individuals used in chemical staining of statoliths for the determination of ring periodicity.

Species	Number of individuals	Chemical used	Technique employed	Reference
Illex illecebrosus	4	strontium	given with food	HURLEY et al., 1985
Illex illecebrosus	8	strontium-tetracycline	with food, force feeding	DAWE et al., 1985
Alloteuthus subulata	11	tetracycline	injection	Lipinski, 1986
Idiosepius pygmaeus	6	tetracycline	ambient exposure	Jackson, 1989
Sepioteuthis lessoniana	7	tetracycline-calcein	ambient exposure	Jackson, 1990
Loliolus noctiluca	9	tetracycline	ambient exposure	Jackson, this report
Loligo chinensis	2	tetracycline	injection	Jackson, this report

(JACKSON, 1989) and juvenile *Sepioteuthis lessoniana* (JACKSON, 1990). However, larger more active species are too sensitive for this type of method, and such other techniques as injection (LIPINSKI, 1986) or inclusion of a statolith-staining drug in the food have been used (DAWE *et al.*, 1985; HURLEY et al., 1985).

Evidence for daily periodicity in statolith growth rings, derived from chemical marking experiments, now exists from 47 individuals out of five species of squids and one sepioid (Table 3). There is considerable scope to extend ring validation work to other cephalopod species, as the species that have been worked on represent only a minute portion of the total cephalopod fauna. Ring validation work on the larger oceanic squids is particularly needed as statolith growth ring analysis promises to be one technique that can be used to establish important biological parameters for many of these species. Furthermore, it is necessary to increase the sample size of validated individuals to extend age validation work beyond the scope of preliminary findings.

It can only be assumed that the statolith ring deposition process that has been observed for *Loliolus noctiluca* and *Loligo chinensis* under these artificial conditions is similar to what occurs in the natural environment. The maintenance conditions were especially suitable for providing a good environment for statolith incremental growth, since the tanks were located outside and thereby exposed to the natural diel light regime. Furthermore, the tanks were relatively large, which promoted a more natural behavior of the squids, especially *Loliolus noctiluca* that appeared to live and grow relatively undisturbed in the tanks. The demonstration of daily statolith rings in *Loliolus noctiluca* and *Loligo chinensis* indicates that these structures will be useful in determining important age and growth parameters for these tropical squids.

ACKNOWLEDGMENTS

I thank J. H. Choat for assistance during the project and in preparation of the manuscript and F. Hoedt for assistance with field collections. I further thank C. C. Lu, who assisted with taxonomic identification of the species studied. This research was supported by grants through James Cook University of North Queensland.

LITERATURE CITED

- BALCH, N., A. SIROIS & G. V. HURLEY. 1988. Growth increments in statoliths from paralarvae of the ommastrephid squid *Illex* (Cephalopoda: Teuthoidea). Malacologia 29:103– 112.
- CAMPANA, S. E. & J. D. NEILSON. 1985. Microstructure of fish otoliths. Canadian Journal of Fisheries and Aquatic Sciences 42:1014–1032.
- DAWE, E. G., R. K. O'DOR, P. H. ODENSE & G. V. HURLEY. 1985. Validation and application of an ageing technique for short-finned squid (*Illex illecebrosus*). Journal of Northwest Atlantic Fishery Science 6:107-116.
- HURLEY, G. V. & P. BECK. 1979. The observation of growth rings in statoliths from the ommastrephid squid *Illex illecebrosus*. Bulletin of the American Malacological Union, Inc., for 1979:23-25.
- HURLEY, G. V., P. H. ODENSE, P. K. O'DOR & E. G. DAWE. 1985. Strontium labelling for verifying daily growth increments in the statolith of the short finned squid (*Illex illecebrosus*). Canadian Journal of Fisheries and Aquatic Sciences 42:380-383.
- JACKSON, G. D. 1989. The use of statolith microstructures to analyze life-history events in the small tropical cephalopod *Idiosepius pygmaeus*. Fishery Bulletin, U.S. 87:265-272.
- JACKSON, G. D. 1990. Age and growth of the tropical nearshore loliginid squid *Sepioteuthis lessoniana* determined from statolith growth ring analysis. Fishery Bulletin, U.S. 87. In press.
- KRISTENSEN, T. K. 1980. Periodical growth rings in cephalopod statoliths. Dana 1:39–51.
- LIPINSKI, M. 1986. Methods for the validation of squid age from statoliths. Journal of the Marine Biological Association of the U.K. 66:505-524.
- LU, C. C., C. F. E. ROPER & R. W. TAIT. 1985. A revision of Loliolus (Cephalopoda; Loliginidae), including L. noctiluca, a new species of squid from Australian waters. Proceedings of the Royal Society of Victoria 97:59-85.
- NATSUKARI, Y., T. NAKANOSE & K. ODA. 1988. Age and growth of loliginid squid *Photololigo edulis* (Hoyle, 1885). Journal of Experimental Marine Biology and Ecology 116:177–190.
- RADTKE, R. L. 1983. Chemical and structural characteristics

of statoliths from the short-finned squid *Illex illecebrosus*. Marine Biology 76:47-54.

- ROPER, C. F. E., M. J. SWEENEY & C. E. NAUEN. 1984. Cephalopods of the world. FAO fisheries synopsis. No. 125, vol. 3. Rome: FAO. 277 pp.
- ROSENBERG, A. A., K. F. WIBORG & I. M. BECH. 1981. Growth of *Todarodes sagittatus* (Lamarck) (Cephalopoda, Omma-

strephidae) from the Northeast Atlantic, based on counts of statolith growth rings. Sarsia 66:53-57.

YANG, W. T., R. F. HIXON, P. E. TURK, M. E. KREJCI, W. H. HULET & R. T. HANLON. 1986. Growth, behavior, and sexual maturation of the market squid, *Loligo opalescens*, cultured through the life cycle. Fishery Bulletin, U.S. 84: 771-798.

The Eastern Pacific Species of the Bivalve Family Spheniopsidae

by

EUGENE V. COAN

Department of Invertebrate Zoology, California Academy of Sciences, Golden Gate Park, San Francisco, California 94118, USA

Abstract. The Spheniopsidae contains only a few fossil and at least four uncommon living species. The type species of Spheniopsis, S. scalaris, from the middle Oligocene of Germany, is discussed and figured. Spheniopsis frankbernardi, a new species, is described from the Panamic province and compared to S. mississippiensis from the lower Oligocene, S. americana from the early Miocene, and S. triquetra from the Recent fauna, all of the eastern United States. Grippina californica occurs from California to Costa Rica; G. berryana is a synonym. Grippina aupouria (Powell, 1937) occurs in New Zealand. Recent spheniopsids probably all brood their young.

INTRODUCTION

Among the materials on the work table of the late Frank R. Bernard were some notes about the Recent eastern Pacific species of the Spheniopsidae. He noted that some lots represented a new species, which is here named for him. As evidenced in a draft manuscript, Bernard intended to erect a new family based on *Grippina*. I have examined this question and decided against doing so.

In a handbook on geology by WALCHNER (1846–1851), a listing of the fossils from the middle Oligocene of the Mainz Basin in Germany was provided by BRAUN (1851). Here Braun (p. 1114) made available, with a minimal description¹ and no figure, a new, minute species of *Corbula*, *C. scalaris*. Its type locality is "Weinsheim" (Weinheim, near Alzey, Rheinland-Pflaz), Germany (49°45'N, 8°6'E).²

In his treatment of the Mainz Basin fauna, SANDBERGER (1861:pl. 22, fig. 1–1b; 1863:286) established a new genus, *Spheniopsis*, for *Corbula scalaris*, which he illustrated with three line drawings.³ NEUFFER (1973:86–87; pl. 9, figs. 3, 4a–b) discussed this species, based in part on Sandberger's

material. Additional species of this genus have been described from the Oligocene of Germany; NEUFFER (1973) lists these, including the similar *S. curvata* KOENEN (1894: 1313–1315; pl. 92, figs. 9a, b, 10a–c, 11a–c) from the lower Oligocene.⁴

Through the kindness of Dr. Ronald Janssen of the Natur-Museum in Senckenberg, I was able to examine and photograph specimens of Spheniopsis scalaris from its type locality (SMF 308 404a, b) (Figure 1). The shells of this species, which attain a length of about 4 mm, are elongate, with a pointed, truncate posterior end. Both valves have about 11 conspicuous, rounded concentric ribs, with wide interspaces. The ribs are lower dorsally and posteriorly. The posterior end has two radial ribs, one just below the posterodorsal margin and a second just ventral to this; the area between them is smooth and produced posteriorly to form the truncate end. The dorsal posterior ridge sets off a conspicuous, smooth escutcheon; the lunule is smooth, but less demarcated. The right valve has a short, peglike anterior tooth on the medial end of a thin, subdorsal ridge, and an elongate posterior tooth⁵; the anterodorsal margin of the left valve fits into a groove just above the short anterior tooth. On the hinge plate between the teeth is a shallow, posteriorly directed resilifer. There is no nymph

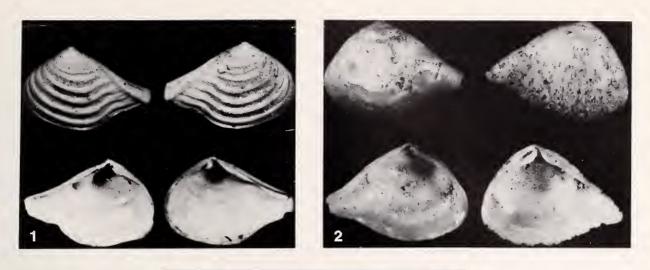
¹ "Corbula scalaris A. Braun. Very small (1.5^{*m*} long) [3.3 mm], rostrate, step-like ribbed species, related to Corbula cuspidata Brongn. Phil.: sand near Weinsheim; very rare."

² Not to be confused with Weinheim, Baden-Würtemberg. This species was incorrectly listed by KEEN (1969:699) as being from Austria.

³ The genus is first made available on the explanation to plate 22, which appeared in 1861.

⁴ KEEN (1969:699) lists this genus as occurring as early as the middle Eocene, but I am unable to locate any records in Europe or North America earlier than the early Oligocene (R. Janssen and D. Dockery, in letters, 8 December and 29 November 1989, respectively).

⁵ I do not know whether these teeth should be called cardinals or laterals, and so I have avoided both terms.





Explanation of Figures 1 to 3

Figure 1. Spheniopsis scalaris, SMF 308 404a, right valve; SMF 308 404b, left valve; middle Oligocene; Weinheim, Rheinland-Pfalz, Federal Republic of Germany; length of each, 2.7 mm.

Figures 2, 3. Spheniopsis americana. Figure 2: USNM 445737 (right valve) and USNM 445738 (left valve), paralectotypes figured by DALL (1903); length of each, 3 mm. Figure 3: USNM 114679, lectotype herein, right valve, length, 2.6 mm; USNM 445736, left valve, paralectotype, length, 2.9 mm.

for the attachment of an external ligament. In the left valve, there is a socket for the anterior tooth; the posterior valve edge rests between the dorsal margin of the right valve and its elongate posterior tooth. There is a short, broad pallial sinus.

MEYER (1887:53-54, 56; pl. 3, figs. 16-16b) described Mikrola mississippiensis, a new genus and species, from the lower Oligocene and Bluff Formation of Mississippi. He compared it to Spheniopsis, stating that the dentition of the right valve was "entirely different." For many years, Mikrola remained a mystery because of Meyer's sketchy figures, and KEEN (1969:637) synonymized it with the semelid genus Cumingia. DOCKERY (1982:100-101; pl. 51, figs. 9-15) illustrated two syntypes of M. mississippiensis (USNM 645099, 645100) and other material, and synonymized Mikrola with Spheniopsis. The posterior tooth in the right valve of this species is much shorter than that in Spheniopsis scalaris, its posterior end is less produced, and the posterior slope is not set off by radial ridges. Other workers may choose to recognize Mikrola as a separate genus or subgenus based on these differences. Spheniopsis mississippiensis, which attains only about 3 mm in length, has about 15 conspicuous concentric ribs on each valve.

Spheniopsis mississippiensis, with its relatively short posterior tooth, is close to the only other North American fossil species in this genus, S. americana DALL (1903:1508; pl. 57, figs. 28, 29), from the Chipola Formation of Calhoun County, Florida. Dall regarded this formation as being of Oligocene age, but it is now regarded as being of early Miocene age (VOKES, 1989). Spheniopsis americana has fine concentric sculpture. The type material consisted of six syntypes. Dall figured the two largest specimens (USNM 445737 and 445738), both measuring 3 mm; because of their slightly different shapes and differing patterns of wear (Figure 2), they probably do not represent a pair. Because both of these valves are significantly eroded, I here select as lectotype a somewhat smaller right valve, measuring 2.6 mm, that is in good condition and shows the characters of the species (USNM 114679), figuring it with a paralectotype left valve in equally good condition (USNM 445736) (Figure 3). The remaining two paralectotypes are USNM 445739 and 445740.

In her discussion of *Spheniopsis americana*, GARDNER (1928:236–237; pl. 36, figs. 9, 10) established a new family for this genus on the grounds that it is distinct from the Corbulidae, species of which have a projecting resilifer in the left valve and a sunken one in the right valve.

Spheniopsids are always minute, and examination of a dried animal of the Recent eastern Pacific Grippina californica (LACM 72-120.1) shows that at least this species broods its young; it is not unreasonable to assume that they all do. They may thus represent a line of brooders derived from the Corbulidae, a family that is known from the Upper Jurassic (KEEN, 1969:692). Spheniopsids have remained small, as is the case with many other bivalve brooders, such as members of the Cyamioidea, Galeommatoidea, Condylocardiidae, Bernardinidae, and Turtoniidae, and some Carditidae and Veneridae (see list in SHASTRY, 1979, and family reviews in Boss, 1982). None of the material presently available of eastern Pacific members of this family is suitable for further anatomical analysis.

The ligament of Recent spheniopsids seems very solid (Figure 12a) and calls to mind the lithodesma of some members of the Thracioidea and the Galeonmatoidea, but further study would be required to demonstrate whether it is calcified.

After this paper was accepted for publication, I learned from Dr. Donald R. Moore (verbal communication, 7 June 1990) that three or four living species of "*Spheniopsis*" in the western Atlantic are currently under study. Indeed, a name is available for one of these: *Montacuta triquetra* VERRILL & BUSH (1898:782–783, 894; pl. 91, fig. 3), which has yet to be adequately illustrated, from 79 m off Cape Hatteras, North Carolina.

EASTERN PACIFIC TAXA

Superfamily MYOIDEA

Family SPHENIOPSIDAE Gardner, 1928

- Spheniopsis SANDBERGER, 1861:pl. 22, fig. 1–1b [1863: 289]
 - Type species: Corbula scalaris Braun, in WALCHNER, 1851:1114; by monotypy.
 - =Mikrola Meyer, 1887 [Type species: M. mississippiensis Meyer, 1887; by monotypy].

Shell elongate, posterior end produced, truncate. With anterior and posterior teeth in the right valve; posterior tooth elongate to short; left valve without teeth; laterally elongate ligament present. Sculpture of fine to coarse concentric ribs, sometimes with radial rays defining posterior slope. Pallial sinus short, broad.

Spheniopsis frankbernardi Coan, sp. nov.

(Figures 4-6)

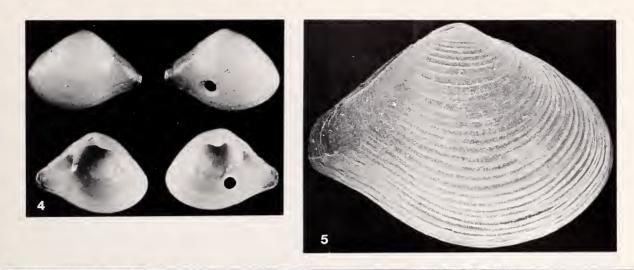
Description: Shell small (to 3.2 mm; holotype), thick, elongate, sharply rounded anteriorly; produced, with rounded truncation posteriorly. Surface with fine concentric sculpture (15–35 ribs; holotype with 30–35 ribs). Right valve with short, thick anterior and posterior teeth on medial ends of subdorsal lamellae, with anterior lamella longer; short, posteriorly oblique resilifer on hinge plate between teeth. Left valve with narrow dorsal margins, without teeth, fitting into subdorsal grooves of right valve. Lunule and narrow, sharply defined escutcheon present. Pallial sinus short, broad.

Type material: LACM 2427, holotype, pair; length 3.2 mm; height. 2.3 mm; convexity, 2.0 mm (Figure 4). LACM 2428, paratype A; length, 2.5 mm (Figure 5). LACM 2429, paratype B; length, 2.6 mm (Figure 6).

Type locality: Off Cabo San Lucas, Baja California Sur (22°8'N, 110°W); 18–37 m, on sand; P. Oringer and L. Marincovich, 4 April 1966; LACM Loc. 66-14.

Distribution: From Punta San Pablo, on the Pacific Coast of Baja California Sur (27°12′55″N, 114°27′30″W) (LACM 71-177.1), to Cabo San Lucas (type locality), into the Gulf of California as far north as Puertecitos, Baja California [Norte] (30°20′N, 119°39′W) (LACM 64-31.1), and south to Playas del Coco, Guanacaste Province, Costa Rica (10°33′N, 85°42′W) (Skoglund Coll.); 13–91 m (mean, 38 m); the only bottom type recorded—on just two lots—is sand. I have examined 11 lots.

- Referred material: LACM 71-177.1—Punta San Pablo, Baja California Sur; 21-24 m, on sand; 1 specimen.
- LACM 71-178.2—Punta San Pablo, Baja California Sur; 21–30 m; 1.
- LACM 2427-2429—Type lot—LACM Loc. 66.14—Cabo San Lucas, Baja California Sur; 18-37 m; 3.
- CAS 068038—Isla Partida, near Isla Espíritu Santo, Baja California Sur; 91 m; 1. Cited by KEEN (1971) as *Grippina berryana*.
- LACM 37-191.1—Isla Tortuga, Baja California Sur; 82 m; 3.
- SBMNH 35150—Bahía de Los Angeles, Baja California [Norte]; 15–29 m; 5.
- SBMNH 35151—Bahía de Los Angeles, Baja California [Norte]; 22–38 m; 3.
- LACM 64-31.1—Puertecitos, Baja California [Norte]; 7-18 m; 1.





Explanation of Figures 4 to 6

Figures 4-6. Spheniopsis frankbernardi Coan, sp. nov., herein. Figure 4: holotype, LACM 2427; length, 3.2 mm. Figure 5: paratype A, LACM 2428; length, 2.5 mm. Figure 6: paratype B, LACM 2429; length, 2.6 mm.

SBMNH 35152—Teacapan, Sinaloa; 51-60 m; 2. Skoglund Coll.—Bahía Santiago, Colima; 6-30 m; 5. Skoglund Coll.—Playas del Coco, Guanacaste Province, Costa Rica; 30-37 m; 2.

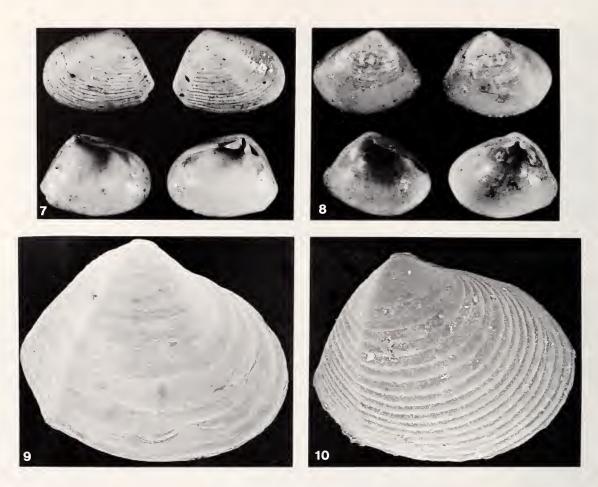
Discussion: This species differs from *Spheniopsis scalaris* and *S. curvata* in having a thicker shell, less elevated concentric ribs, a less produced and less abruptly truncate posterior end, a posterior slope not defined by radial ribs, and a shorter posterior tooth in the right valve. It differs from *S. mississippiensis* in having less elevated concentric ribs and a less produced posterior end. It differs from *S. americana* in having a thicker shell, a less produced posterior end, and more conspicuous sculpture. It differs from *S. triquetra*, which is thus far known only by the holotype (USNM 77627), a pair measuring 2 mm in length, in being larger, proportionately longer and heavier, in having thicker, more ventrally directed teeth in the right valve, and in retaining sculpture on its umbones. More detailed study of western Atlantic material (D. R. Moore, in preparation) should provide additional points of comparison.

Grippina DALL, 1912:128.

Type species: *G. californica* DALL, 1912:128; by original designation.

Similar to *Spheniopsis* but with a broadly truncate posterior end that is not produced. Posterior slope defined by two low radial ridges. With short anterior and posterior lateral teeth in the right valve; left valve without teeth. Sculpture of fine to coarse concentric ribs, or smooth. Pallial sinus short, broad.

This genus is thus far known from the Pleistocene and Recent faunas in the eastern Pacific and the Recent fauna of New Zealand.



Explanation of Figures 7 to 10

Figures 7-10. Grippina californica. Figure 7: holotype of G. californica, USNM 214362; length, 2.6 mm. Figure 8: holotype of G. berryana, CAS 064756; length, 2.3 mm. Figure 9: LACM 72-114, northwest end of Isla Cedros, Baja California [Norte]; 14 m; length, 2.0 mm. Figure 10: SBMNH 35153, Cuastecomate, Jalisco, Mexico; 12-30 m; length, 1.8 mm.

Grippina californica Dall, 1912

(Figures 7-12)

Grippina californica DALL, 1912:128; OLDROYD, 1925:205; pl. 15, figs. 1—3; LAMY, 1941:15, unnumbered fig. Grippina berryana KEEN, 1971:269-270, 943; fig. 693.

Type material and localities: *G. californica*—USNM 214362, holotype, pair; length, 2.6 mm; height, 2.0 mm; thickness, 1.4 mm (Figure 7). Off San Diego, San Diego Co., California (32°40'N, 117°14'W); 29–37 m; C. W. Gripp.

G. berryana—CAS 064756, holotype, pair; length, 2.3 mm; height, 1.9 mm; convexity, 1.4 mm (Figure 8); CAS 064757, paratype, worn left valve; SBMNH 34819, paratype, one worn pair. Northwest side of Bahía Salinas, Isla Carmen, in the Gulf of California, Baja California Sur (25°59'N, 111°8'W), in 5–9 m; J. Fitch.

Description: Small (to 2.8 mm; CAS 068036; Isla Guadelupe, Baja California [Norte]), quadrate to trigonal; posterior end broadly truncate, not greatly produced. Sculpture somewhat variable, with heavy concentric ridges in some specimens, almost smooth in others. With short anterior and posterior teeth in right valve, and with anterior tooth on medial end of long subdorsal lamella; posterior end without such a lamella; narrow, posteriorly oblique resilifer present between teeth; left valve without teeth. Pallial sinus short, broad.

Additional specimens are illustrated with SEM micrographs (Figures 9–12).

Distribution: Southeast of Santa Cruz Island, Santa Barbara Co., California (33°55'47"N, 119°31'5"W) (LACM 48-43.2), to northwest end of Isla Cedros, Baja California [Norte] (28°21'N, 115°15'W) (LACM 72-114); in the Gulf of California as far north as Punta Gorda, Baja California







Explanation of Figures 11 and 12

Figures 11, 12. Grippina californica. Figure 11: LACM 71-93, southeast end of Isla Cedros, Baja California [Norte]; 73-91 m; length, 2.3 mm. Figure 12: SBMNH 35153, Cuastecomate, Jalisco, Mexico; 12-30 m; length, 2.0 mm; Figure 12a: close-up of right valve showing ligament between teeth; view is oblique from anterior end.